Cirral Activity and Feeding in the Lepadomorph Barnacle *Lepas pectinata* Spengler (Cirripedia)

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Among the lepadids, *L. pectinata* shows extreme adaptation to neustonic life, as a small species inhabiting fragile, ephemeral objects at or near the water surface. In addition to feeding by cirral extension on small macroplankton, *L. pectinata* employs rhythmic cirral beating in continuous feeding on microplankton. The form and setation of the cirri and mouthparts are adapted to these dual modes of feeding. The rhythmic cirral activity of *L. pectinata* is in the opposite mode to that of balanoids, the cirri being held extended between beats, and is similar in general to that of *Verruca stroemia*. All three patterns of cirral activity have evolved independently, those of *L. pectinata* and *V. stroemia* being convergent, associated with feeding on microplankton.

Other features of adaptation of *L. pectinata* to its mode of life are discussed. They include, in addition to continuous versatile feeding on small food organisms in the top few centimetres of the water, a rapid growth rate, onset of sexual maturity and reproduction at a small size, insensitivity of the cirri to light, water movements or contact stimulation, production of specialized flotatory nauplii, settlement of cyprids gregariously on planktonic objects and a precocious post-settlement metamorphosis.

INTRODUCTION

Although lepadid barnacles are well known taxonomically (Darwin, 1851; Nilsson-Cantell, 1921; Stubbings, 1963; Zullo, 1963; Utinomi, 1968; Newman, 1972; Arnaud, 1973; Foster, 1978), only a few scattered reports have been given of their feeding activities. In general, these place emphasis on prolonged cirral extension and macrophagy (Gruvel, 1893; Howard and Scott, 1959; Patel, 1959; Bieri, 1966; Crisp, 1967; Jones, 1968; Lockwood, 1968; Cheng and Lewin, 1976), with some intimation of cooperative feeding on larger prey. The obvious and prolonged extension of the cirri in *Lepas* species is also attested by the many photographs in elementary textbooks and popular accounts of marine animals, showing *Lepas* with its cirri fully exposed. No other cirripede behaves so readily in this way. *Lepas* is often said to be a generalized thoracican genus, but all aspects of its biology are indicative of specialization for a neustonic mode of life. This specialization is nowhere more evident that in the small *L. pectinata* of tropical and warm temperate waters, a species whose cirral activity and feeding have hitherto been undescribed.

L. pectinata preferentially attaches to a variety of small, fragile floating objects such as cuttle bones, feathers, sargassum, pumice and tar (Darwin, 1851; Horn, Teal and Backus, 1970; Lang, 1979). The present paper analyses the cirral activity of *L. pectinata* in relation to cirral and mouthpart anatomy and offers some comparisons with feeding in other species of the genus in the same neustonic habitat.

MATERIALS AND METHODS

Living specimens of *L. pectinata* attached to a cuttlefish shell were collected by Mr M. J. Moran at Cape Banks, Botany Bay, N.S.W. in October, 1978. The animals

were maintained in an aerated aquarium tank at the University of Sydney. Cinematographic records of cirral activity and details of anatomical structure were obtained by methods described in previous papers (Anderson, 1978, 1980a). Anatomical details were determined from specimens preserved in 5% formalin in sea water, dissected, and examined by both bright field and dark field microscopy of unstained material. Records of cirral movements were made by cinephotomacrography, using Kodak Ektachrome 160 super 8 mm film, and analysed using a Eumig R2000 analysing projector. No food was provided for the living *L. pectinata* during the two weeks that they were kept alive in the tank, but the water was renewed every three days. After 10 days in the tank, some of the animals released large numbers of nauplius larvae, on which the captive population proceeded to feed. It was notable, however, that the level and pattern of activity was no greater when nauplii were present than it had been in the absence of obvious food organisms. Since all of the animals in the tank retained their vigour throughout the two weeks of observation, it was presumed that they were able to feed microphagously on naturally occurring microscopic organisms in the water. As will be shown below, the cirral and mouthpart morphology, the mode of cirral activity and the gut contents bear out the fact that *L. pectinata* is both a microphagous and macrophagous feeder in the neuston.

OBSERVATIONS

General External Anatomy. The general external anatomy of *L. pectinata* is well known. (Darwin, 1851; Foster, 1978) and only certain aspects will be emphasized here. The species is the smallest in the genus *Lepas*, with individuals rarely exceeding 12 mm in length. The grey-coloured capitular plates (Fig. 1A) are thin and deeply cupped, with closely approximated margins. The distinctive ridging on the plates and
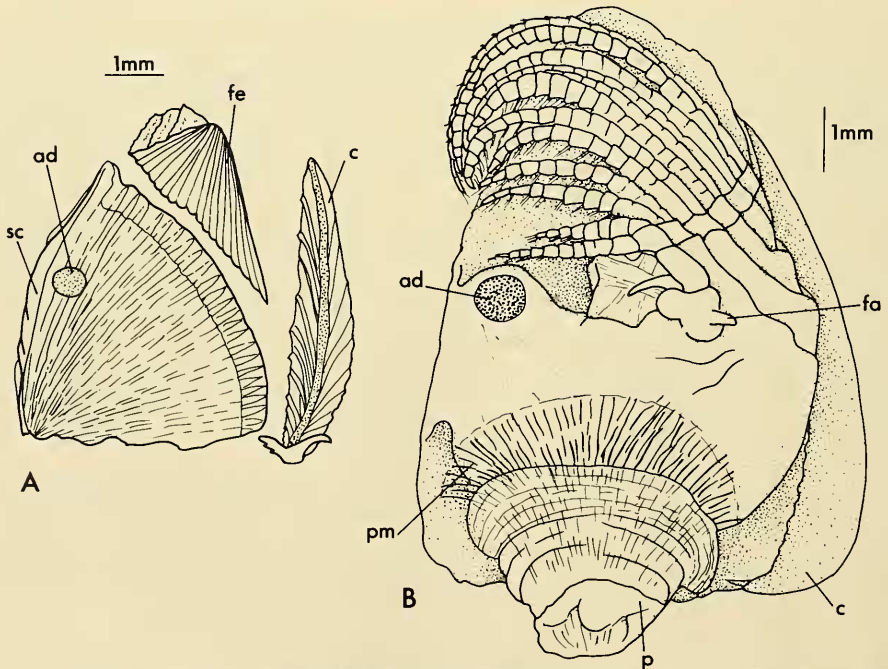

Fig. 1. A. — The carapace plates of *L. pectinata*; interior view of the left scutum, left tergum and carina. B. — *L. pectinata,* viewed from the right side, with the right valve removed. *ad,* adductor scutorum; *c,* carina; *fa,* filamentary appendage; *p,* peduncle; *pm,* peduncular muscle; *sc,* scutum; *te,* tergum.

the positions of the umbones reveal the specialized growth pattern which yields the globose, lightweight valves. The capitulum is also large relative to the peduncle, which is short (Fig. 1B), cone shaped, thin walled and muscular. The yellowish covering of the peduncle is irregularly annulated but otherwise smooth and not setose. Longitudinal muscle strands are conspicuous beneath the peduncular cuticle in preserved specimens, fanning out into the mantle beneath the basal margin of the scutum of each side (Fig. 1B).

Within the capitular valves, the body of the animal is relatively large, almost completely filling the mantle cavity when in the retracted position with the cirri curled (Fig. 1B). The prosoma is swollen and thin walled, with the musculature and other internal organs clearly visible through the cuticle. The oral cone is large and the thorax well developed. The cirri are of moderate length, but strongly formed for the size of the animal. The first pair is set quite close to the second pair on either side of the posterior end of the oral cone (see also Fig. 4A).

In contrast to the relatively large size of the body, the adductor scutorum muscle is quite small (Figs 1A and 1B). It lies close to the occludent margins of the scuta, approximately at the midpoint of the length of these margins. The aperture, which lies apical to the adductor scutorum, thus occupies only the apical half of the rostral surface of the capitulum (Fig. 4B). When extended, the body and limb bases of the animal fill the aperture. When withdrawn, the coiled limbs are only just confined within the aperture. As will be shown below, the large body, small adductor, small aperture and restricted mantle cavity of L. pectinata are associated with a mode of life in which the animal spends most of its time with the body and limbs extended in the water and only occasionally retracts within the shell. The contrast between the bold exposure of the limbs in living L. pectinata and the fugitive retreat of most barnacles into the mantle cavity at the slightest provocation is perhaps the most striking indication of the adaptation of L. pectinata to a highly specialized mode of neustonic life.

Anatomy of the Cirri. As in all species of *Lepas,* cirrus I in *L. pectinata* shows substantial modification as a maxilliped. Cirrus II is partially modified anatomically for this function and the remaining cirri (III-VI) show a more generalized form. In the following description, setal directions refer to the position of the limbs when the animal is withdrawn into the mantle cavity as in Fig. 1B.

Cirrus I (Figs 2A and 2B) has moderately short, subequal rami, the exopod having 11 or 12 podomeres, the endopod 9. Apart from the terminal few, the podomeres of both rami are short and broad. Setation is sparse on the lateral surfaces, being confined to a few setae on the distal margins of the podomeres, but dense on the median surfaces of both rami. On the exopod, the median setae of the distal five podomeres arise at the distal margins of the podomeres, point distally and are simple setae. On the remaining podomeres, dense brushes of long, thin, serrate setae arise from the posteromedian surfaces and point posterodistally. On the endopod, dense brushes of similar long, thin serrate setae arise from the median surfaces of the podomeres and point anteriorly, intermeshing with the median setae of the exopod. Little setation occurs on the protopod except for a bunch of long, distally directed setae distally on the median surface.

Cirrus II (Figs 2C and 2D) has longer, more cylindrical rami than cirrus I, the exopod and endopod being almost equal in length, with 12 and 14 podomeres respectively. As in cirrus I, lateral setation is sparse and median setation dense, especially on the proximal half of each ramus. These median setae are a mixture of simple and serrate, long, thin setae all pointing anteriorly and overlapping with the median setae of cirrus I.
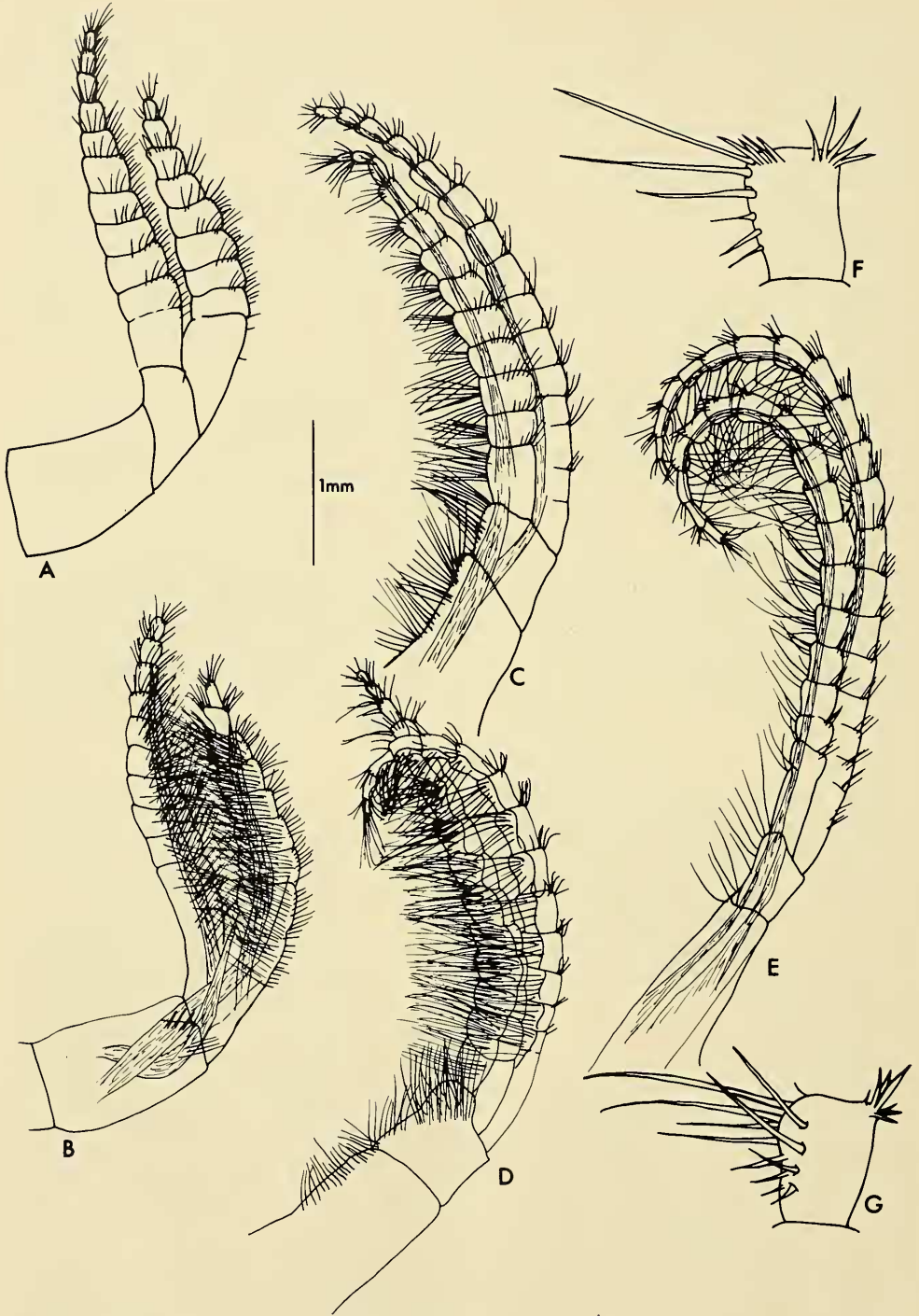
Fig. 2. L. pectinata. A. — Cirrus I, right lateral view. B. — Cirrus I, left, median view. C. — Cirrus II, right, lateral view. D. — cirrus II, left, median view. E. — Cirrus III, right, lateral view. F. — Podomere 10 of exopod of right cirrus III, lateral view. G. — Podomere 10 of exopod of left cirrus III, median view.

The remaining cirri, III-VI, all have long cylindrical rami. Podomere numbers for the exopod and endopod are 18/20, 19/21 and 22/19 respectively (Figs 2E and 3A). Each podomere carries 6 pairs of setae anteriorly, the distal 3 pairs being long (Figs 2F and 2G), and a group of short setae posteriorly on the distal margin. Most of the setae are simple, but serrate setae occur amongst them on the more proximal podomeres of the limbs. The long anterior setae of cirri III-VI are about 0.75 mm in length, but when the cirral rami are spread in the extended position shown in Fig. 4, the setae do not meet across the spaces between the distal parts of the rami.

Anatomy of the Mouthparts. The oral cone of *L. pectinata* (Fig. 3B) is large and prominent. The bullate labrum is densely setose around the entrance of the preoral cavity, the setation being continued along the posteromedian margins of the mandibular palps (Fig. 3D). Mandibles, maxillules and maxillae are in the usual array, but their masticatory margins show prominent setation and only moderate
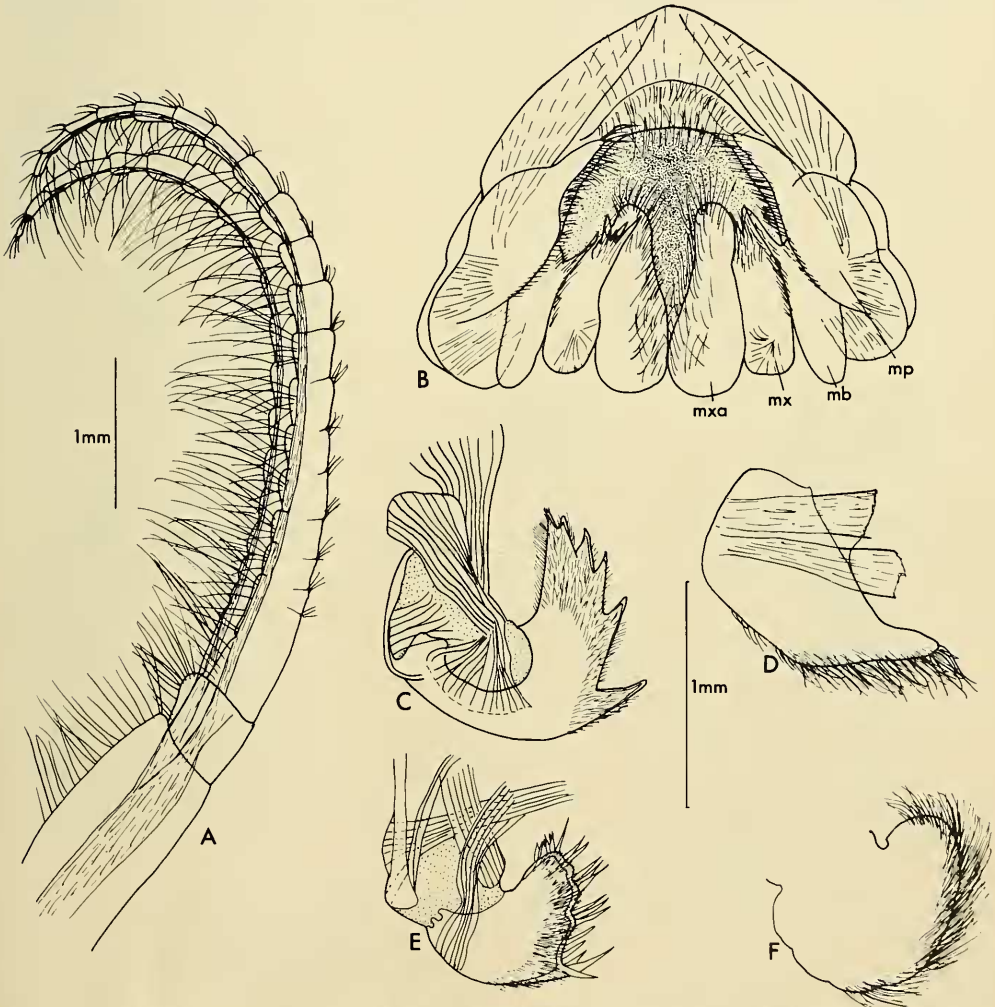

Fig. 3. *L. pectinata*. A. — Cirrus IV, left median view. B. — Oral cone, posterior view. C. — Right mandible, lateral view. D. — Right mandibular palp, lateral view. E. — Right maxillule, lateral view. F. — Right maxilla, lateral view. *mb*, mandible; *mp*, mandibular palp; *mx*, maxillule; *mxa*, maxilla.

spination. The mandible (Fig. 3C) has 5 teeth, but the incisor tooth is modest and the molar process is small. The maxillule (Fig. 3E) shows only vestigial stepping of the margin, small cutting blades on the lateral angle and short spines on the median angle. The maxilla (Fig. 3F) is a convex lobe with many fine, anteriorly directed setae on the free margin. These mouthparts, while retaining the capacity for maceration of small prey, are also indicative of an ability to retain and process fine particulate food (compare *Semibalanus balanoïdes* and *Verruca stroemia*; Stubbings, 1975; Anderson, 1980a).

Cirral Activity. The most striking feature of the cirral activity of *L. pectinata* is that the animals are active continuously. The group of individuals observed in the present study showed no break in activity during two weeks. Even in the brief periods when the animals were removed from the aquarium in order to change the water, cirral exposure and movements of the peduncle continued. Activity was maintained in all conditions of illumination, being unaffected by bright light, darkness, or changes of illumination. No shadow reflex could be elicited. Activity was unaffected by water
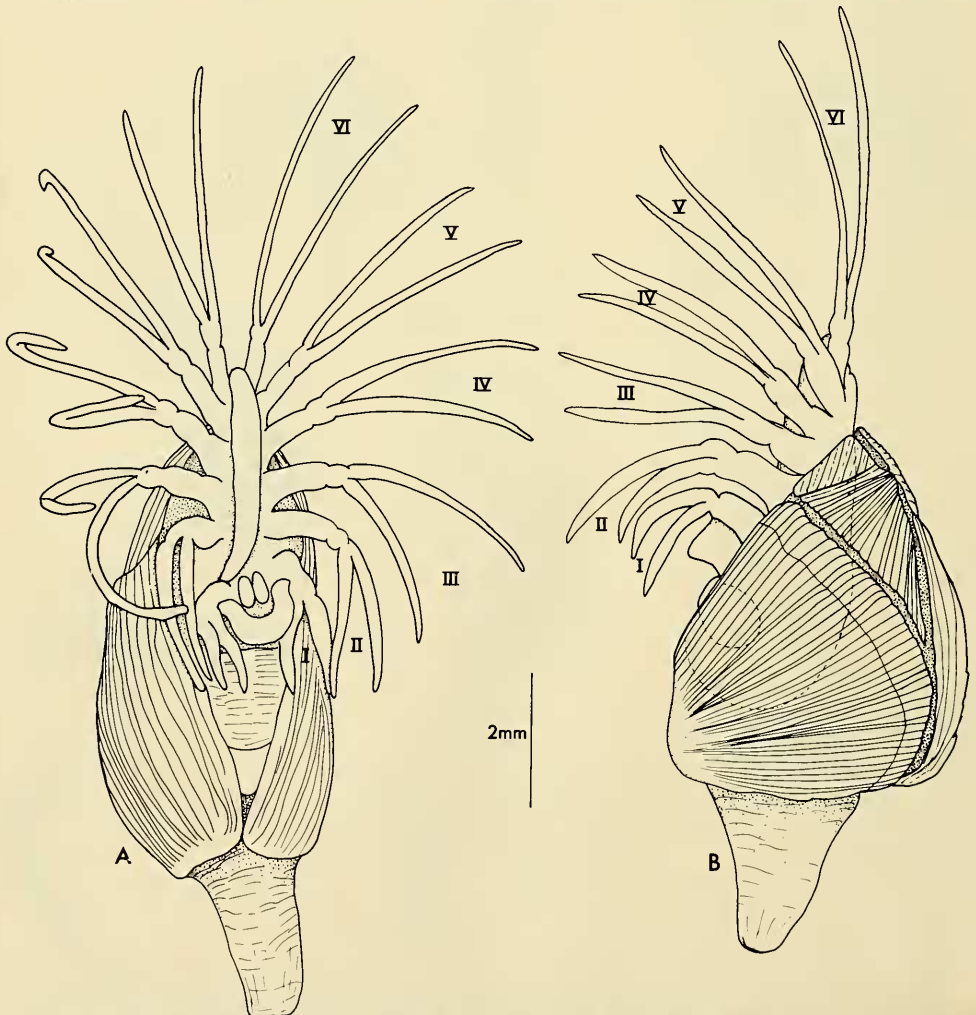

Fig. 4. *L. pectinata,* with cirri fully extended. A. — Ventral view. B. — Lateral view.

movements or by reversing the orientation of the animals relative to the water surface. Animals attached on both sides of the cuttle bone and around its margin continued their activity regardless of orientation. Activity was also unaffected by contact with the water surface. Submerged individuals swept the water with their cirri. Individuals at the water surface swept the surface, with some cirral rami projecting above the surface.

A sharp percussive vibration of the aquarium caused the animals to react by sudden withdrawal into the shell, but only momentarily. The shell valves reopened and the cirri emerged again in a few seconds. In general, the activity of *L. pectinata* at or just under the water surface is one of continuous feeding and low sensitivity to environmental disturbance.

The activity expressed by the animals involves two elements. One is swaying of the capitulum on the short peduncle, both from side to side and back and forth, slowly swinging the extended cirral net about in the water. This swaying action tends to be self sustaining within a group of individuals, in that movement of one causes contact with adjacent animals and elicits movement by them.

The second and more vigorous element of activity in *L. pectinata* is rhythmic cirral extension and withdrawal. The extended position is the normal one for this species. In it, the body is straightened and protruded through the aperture to the level of the oral cone (Fig. 4). Cirri IV-VI stand upright as a fan at the carinal end of the aperture, with cirrus III adjacently upright on either side in a carinolateral position.

Fig. 5. A - E. — Representative cirral positions during a typical sequence of limb extension and withdrawal in *L. pectinata*, seen in lateral view. The total sequence occupies 1.28 s.
A. — Position at the beginning of the sequence
B. — 0.28 s from the beginning of the sequence
C. — 0.5 s
D. — 0.72 s
E. — 0.94 s
F. — 1.28 s

Cirrus II on either side has its rami directed forwards above the oral cone, and cirrus I similarly projects forwards on either side of the oral cone.

From the extended position, the animal makes a regular movement (Fig. 5) of withdrawal of the cirri followed by extension. In the withdrawal movement, the body swings downwards and forwards on the axis of the adductor muscle. The first two pairs of cirri are drawn down into the mantle cavity. Cirri III-VI are folded together and curled forwards, but not completely withdrawn into the mantle cavity. After a short pause, the cirri and body are extended again. The long cirri first uncurl, then extend and spread, accompanied by unfolding and protrusion of cirrus I and II on either side.

Frame by frame analysis of cinematographic records (Fig. 6) shows that the timing of the withdrawal-extension sequence varies little among individuals. At 22 - 23°C,, observations of 3 individuals performing a total of 70 beats gave an average cirral withdrawal time of 0.28 - 0.30 s, followed by a pause of 0.17 - 0.37 s and a cirral protrusion time of 0.36 - 0.40 s. The slight difference in duration between withdrawal and extension of the cirri reflects, as is usual with thoracican barnacles, the faster muscular contraction and slower hydraulic action of the two movements. The range of variation in the duration of the pause with the cirri withdrawn is correlated with the rate of cirral beating in different individuals. At higher rates of beat, the pause in the withdrawn position is of shorter duration, but it was not observed to be greater than 0.37 s even when the rate of beat was markedly slow.

The factors determining the rate of beat are obscure. General observation showed that adjacent individuals in the group under study exhibited different rates of beat. Counts were made for 11 individuals recorded simultaneously on film. The number of beats performed per 10 s by these animals were 0.2, 0.8, 1.7, 2.0, 2.4, 4.75, 5.0, 5.0, 5.9, 7.25 and 7.6 respectively. The range was thus from one beat every 50 s to one every 1.3 s, with corresponding intervals of cirral extension of 49 s and 0.6 s respectively, slight differences in timing being evident from beat to beat. The two
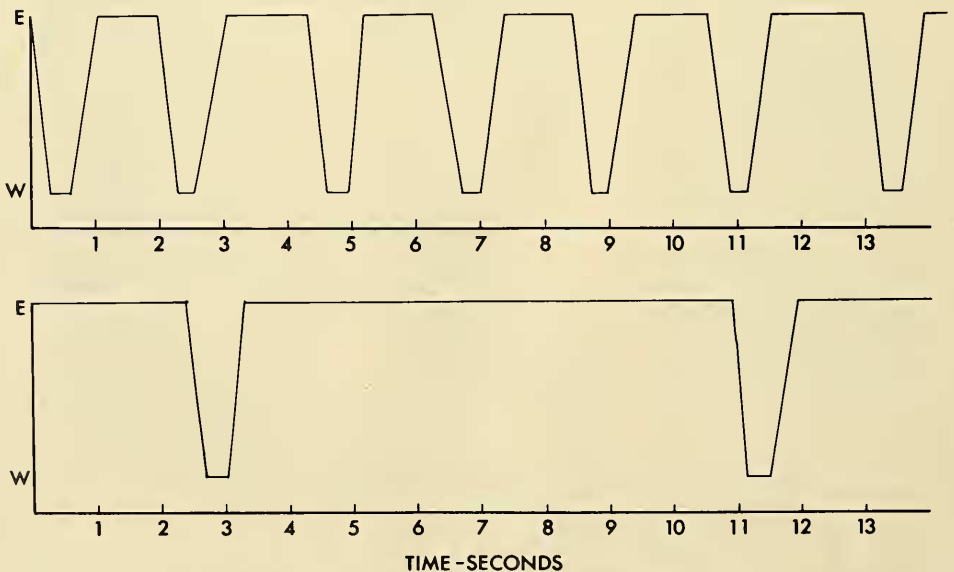

TIME –SECONDS

Fig. 6. Record of cirral extension and withdrawal in two individuals of *L. pectinata* in still water at 22-23°C. Vertical axis: E. limbs extended, W. limbs withdrawn. A. — An individual beating at 5 per 10 s. B. — An individual beating at 1.7 per 10 s.

examples given in Fig. 6 show rates of 5.0 and 1.7 beats per 10 s, with average interbeat durations of 1.3 s and 8.4 s respectively.

In spite of these variations in the rate of beat, the withdrawal - extension action is the same in all individuals. On withdrawal, the cirri curl down through the water, collecting suspended particulate matter. During the pause before re-extension, the coiled cirri show movements indicative of cleaning off by the maxillipeds and mouthparts. The cirri are then extended again, preparatory to the next sweep.

When the cirri were extended in water containing nauplii, individual cirral rami were seen to curl forwards and down to be cleaned off by apposition of the second pair of cirri. These limbs were then bent downwards between the first pair of cirri, rubbed together and drawn back. Finally, the endopods of the first pair of cirri were brought together in the midline above the mouthparts and rubbed one upon the other. By this means, the small captured prey are presumably transferred to the mouthparts for ingestion.

Contact of the extended cirri with a larger object such as the end of a pencil elicited a strong grasping action by all the cirri together. *L. pectinata* appears to be able to feed by the capture of larger prey, as well as on small prey and particulate matter.

In order to determine the food intake resulting from these movements, the gut contents of five of the captive individuals were examined. Three categories of food were found in abundance, phytoplankton, nauplii and fragments of adult exuviae. It can be concluded that *L. pectinata* is able to feed, by its rhythmic cirral action, its individual ramal action and the grasping closure of the cirral net, on microplankton and small macroplankton. Little or no selective discrimination of food intake appears to occur, and feeding is continuous at or just below the water surface day and night, irrespective of water movements.

DISCUSSION

Feeding in Lepadids. Prior to the present study, information on cirral activity in *Lepas* was available for *L. anatifera* (Gruvel, 1893; Southward, 1957; Howard and Scott, 1959; Crisp and Southward, 1961; Crisp, 1967), *L. anserifera,* (Bieri, 1966; Jones, 1968), *L. fascicularis* (Crisp, 1967; Cheng and Lewin, 1976) and *L. pacifica* (Cheng and Lewin, 1976). All accounts emphasize a number of common features of lepadid cirral activity. The cirri are held extended for long periods in either still or moving water and are swept through the water by vigorous muscular contractions of the peduncle. On contact with animal food and the stimulus of certain amino-acids and ions (Crisp, 1967), the cirri make two types of response. If the prey is small, contacting a single cirrus, the contacted cirrus curls down, capturing the prey and conveying it to the maxillipeds, thence to the mouthparts. If the prey is large, the cirral net curls as a whole to grasp the food and hold it against the mouthparts. Large prey grasped in this way may be held for up to two hours before the remains are released.

As the present study has shown, *L. pectinata* retains these two feeding responses in spite of its small adult size. The responses are basically like those of scalpellids (Batham, 1946; Barnes and Reese, 1959; Howard and Scott, 1959) but are associated in lepadids with a number of specializations related to the floating neustonic habit. These include prolonged cirral extension in still water, active sweeping by peduncular contractions, and insensitivity to illuminations, water movements or contact stimulation, all of which combine to result in the vigorous capture of small or large planktonic prey. These feeding adaptations are further combined with lightweight, globose capitular valves, a specialized growth pattern, fast

rates of growth (Darwin, 1851; Annandale, 1909b; Evans, 1958; Skerman, 1958), rapid attainment of sexual maturity, flotatory specializations during naupliar development (Bainbridge and Roskell, 1966; Lang, 1979), planktonic searching for floating substrata by cyprids, highly gregarious settlement and, in *L. pectinata* (personal observation), a precocious development of the adult organization post-settlement. An account of the latter phenomenon will be given elsewhere. Without doubt, lepadids are highly specialized among the Lepadomorpha for the catch-as-catch-can inhabitation of floating objects in an opportunistic manner.

The carnivorous propensities of lepadids in this environment are well documented in direct observations on their feeding habits. Howard and Scott (1959) fed *L. anatifera* on *Artemia* and *Tigriopus*, and observed polychaetes, amphipods, carids, gastropods, bivalves and pycnogonids in the guts of field-collected specimens. Patel (1959) and Crisp (1976) fed the same species on pieces of *Mytilus* tissue, which were grasped by the cirral net and engulfed in the manner first described by Gruvel (1893). Bieri (1966) and Jones (1968) have shown that *L. anserifera* is even more active as a carnivore, feeding on whole *Vellela*, pieces of *Physalia* tentacle and pieces of fish and squid. Bieri gave evidence that this species can feed cooperatively, passing a *Vellela* from one individual to the next. *L. fascicularis* has also been observed to eat *Vellela* (Bieri, 1966) and pieces of *Mytilus* tissue (Crisp, 1967). In the natural habitat, it is clear that macrozooplankton is the major food source for the larger *Lepas* species.

Anatomical descriptions of the mouthparts of *L. anatifera, L. anserifera* and *L. fascicularis* support this conclusion. The comparative anatomy of the cirri and mouthparts further indicates a similar diet of macrozooplankton for other lepadids of the same oceanic habitat, *L. testudinata, L. australis, L. pacifica, Conchoderma virgatum* and *C. auritum* (e.g. Hoek, 1907; Nilsson-Cantell, 1921; Petriconi, 1969; Foster, 1978). Powerful mandibles with strong cutting teeth and a prominent molar process, heavily built maxillules with a large cutting spine on the lateral angle, a sequence of setose steps along the cutting edge and a group of strong spines in the median angle, and a strong spinose development of the maxillae, are features of these species. *L. pectinata* retains these features on a smaller scale, but the cutting masticatory processes of the mouthparts are relatively reduced and the mouthparts, mandibular palps and labrum carry many fine setae. This is indicative of an ability to collect and ingest particulate material gathered by the cirri, a fact confirmed by analysis of gut contents. *L. pectinata* feeds on small macroplankton by the usual two lepadid methods, but also takes in substantial quantities of microplankton.

Rhythmic Cirral Activity in **L. pectinata.** It is in connection with particulate feeding that the rhythmic cirral activity of *L. pectinata* can be interpreted. Little reference has been made to such activity in other lepadid species. It has been mentioned as occurring occasionally in *L. anatifera* at a maximum rate of 2.85 contractions per 10 seconds (Southward, 1957) but the pattern and significance of the activity were not described. In *L. anatifera*, the rami of cirrus I and the exopod of cirrus II carry dense setation on the median surface, arranged in a pattern similar to that of *L. pectinata*, but there is no evidence that *L. anatifera* feeds on particulate material. The maxilliped specialization in this species appears to be related to a grasping function.

In *L. pectinata*, in which every individual maintains a rhythm of cirral contractions, albeit at a wide range of rates among individuals (from 1 per 50 s to 1 per 1.3 s in the present study), the cirral movements gather particulate material from the water and transfer it to the maxillipeds. In addition to the rami of cirrus I and the exopod of cirrus II, the endopod of cirrus II in *L. pectinata* carries dense, anteriorly pointing setation. Rhythmic feeding on microplankton can therefore be recognized as

a third feeding mechanism in this species, with correlated setose arrangements on the mouthparts and two pairs of maxillipeds. The continuous performance of this rhythmic activity, the amount of microscopic material in the gut and the ability of *L. pectinata* to remain active and healthy in water containing no macroplankton, confirm the importance of particulate feeding in this species.

The pattern of rhythmic cirral activity is also different from that well known for various balanomorph species. In particular, the timing is reversed as compared with balanids, the cirri being held extended between beats, with only a brief pause in the contracted position during each beat. In balanids, the cirri are held in the contracted position between beats, with little or no pause in the extended position (Crisp and Southward, 1961; Anderson, 1980b). There is also no indication in *L. pectinata* that the rhythmic cirral activity drives a current of water through the mantle cavity, as it does in balanids. Indeed, there is very little free space for such a current in the mantle cavity of *L. pectinata,* though some movement of water across the vascularized internal surfaces of the mantle valves must occur at each beat.

A comparison of the timing of events between the rhythms of *L. pectinata* and a representative balanoid, *Balanus balanus,* emphasizes this contrast and also reveals certain functional constraints in the cirripede cirral mechanism. *B. balanus* shows rhythmic extension and withdrawal at a rate of 2-5 beats per 10 seconds (Crisp and Southward, 1961). The average duration of the pause between beats, with the cirri withdrawn, is 0.8 - 1.74 s. During each beat, cirral extension takes 0.75 - 1.25 s and is immediately followed by a faster withdrawal, taking 0.5 - 1.0 s.

In *L. pectinata*, the cirri may be held extended up to 50 s between beats, but rates of 4-5 beats per 10 seconds are frequently observed. At this comparable rate, cirral extension in 0.38 - 0.40 is followed by a pause of 1.0 - 1.3 s with the cirri extended. Cirral withdrawal in 0.28 - 0.30 s is then followed by a pause of 0.17 - 0.28 s before the cirri are extended again. In both species, cirral extension is slower than cirral withdrawal, a function of the similar hydraulic and muscular mechanisms involved in both cases. Other than this common factor, the rhythms of the two species are performed in entirely different ways. Extension and withdrawal are both faster in *L. pectinata* than *B. balanus*. Between extension and withdrawal, the cirri are held in the mantle cavity for a much shorter time in *L. pectinata* than in *B. balanus*. Following each extension, the cirri are held extended in *L. pectinata* for a period equal to or longer than the duration of a beat. In *B. balanus,* there is no pause in the extended mode. These differences indicate that the rhythmic cirral beating of *L. pectinata* has evolved independently of that of balanoids, lending further support to the view that it is a special feature of *L. pectinata* among lepadids.

The recent description and analysis (Anderson, 1980a) of rhythmic cirral activity in the verrucid *V. stroemia*, again evolved independently of balanoid beating, provides a further opportunity for comparison with *L. pectinata*. In this comparison, the similarities are much greater. *V. stroemia,* like *L. pectinata*, performs rhythmic cirral beating at 4-9 beats per 10 seconds, with the cirri held extended between beats. In each beat, the average duration of the withdrawal movement is 0.34 s, little different from that of *L. pectinata,* and of the extension movement 0.57 s, intermediate between *L. pectinata* and *B. balanus*. The average duration of the pause between beats with the cirri extended is 0.90 s in *V. stroemia,* slightly less than in *L. pectinata*. On the other hand, there is no pause with the cirri in the withdrawn position in *V. ,stroemia*. Once withdrawn, they are immediately extended again. Another unique feature of the rhythmic cirral action of *V. stroemia* is that the long, posterior cirri do not curl forwards during the withdrawal movement.

Thus in spite of the general similarity of the rhythmic cirral action of *V. stroemia*

and *L. pectinata*, the two patterns of action differ fundamentally in the lack of a pause in the withdrawn position in *V. stroemia* and in the lack of cirral bending. The maxillipeds also spread and close in different ways in the two species. Since all phylogenetic considerations point to the independent evolution of these rhythmic actions as specialized features of these species within their genera, the differences between them are not surprising. What is more remarkable is the convergent similarity that they show as modifications of the prolonged cirral extension with captorial feeding characteristic of lepadids and verrucids respectively. *L. pectinata* and *V. stroemia* are both small species adapted to unusual habitats as compared with other members of each genus. *L. pectinata* preferentially inhabits ephemeral objects at the water surface. *V. stroemia* is a shallow water species. Both retain captorial feeding on small macroplankton, but both also feed on microplankton. Both have finely setose mouthparts and maxillipeds. Both capture their microplankton by a rhythmic cirral action in which the cirri are held extended between beats. In view of this convergent evolution of similar rhythmic cirral activity in a lepadomorph and a verrucomorph, the possibility of convergent evolution of the balanoid pattern of rhythmic cirral activity on more than one occasion in the Balanomorpha must not be overlooked.

ACKNOWLEDGEMENTS

References

ANDERSON, D. T., 1978. — Cirral activity and feeding in the coral-inhabiting barnacle *Boscia anglicum* (Cirripedia). *J. mar. biol. Ass. U.K.* 58: 607-626.

——, 1980a. — Cirral activity and feeding in the verrucomorph barnacles *Verruca recta* Aurivillius and *V. stroemia* (O. F. Müller) (Cirripedia). *J. mar. biol. Ass. U.K.* 60 (in press).

——, 1980b. — Cirral activity and feeding in the balanoid barnacle *Balanus perforatus* Bruguière (Cirripedia) (in preparation).

ARNAUD, P. M., 1973. — Le genre *Lepas* Linné 1758, dans les Terres Australes et Antarctiques Françaises (Cirripedia). *Crustaceana* 24: 157-162.

BAINBRIDGE, V., and ROSKELL, J., 1966. — A redescription of the larvae of *Lepas fascicularis* Ellis and Solander with observations on the distribution of *Lepas* nauplii in the Northeastern Atlantic. Pp. 67-81 in H. Barnes (ed.), *Some contemporary studies in Marine Science.* London: Allen and Unwin.

BARNES, H. S., and REESE, E. S., 1959. — Feeding in the pedunculate cirripede, *Pollicipes polymerus* J. B. Sowerby. *Proc. zool. Soc. Lond.* 123, 569-585.

BATHAM, E. J., 1945. *Pollicipes spinosus* Quoy and Gaimard. I. Notes on biology and anatomy of the adult barnacle. *Trans. R. Soc. N.Z.* 74: 359-374.

BIERI, R., 1966. — Feeding preferences and rates of the snail, *Ianthina prolongata*, the barnacle, *Lepas anatifera,* the nudibranchs, *Glaucus atlanticus* and *Fiona pinnata*, and the food web in marine neuston. *Publs. Seto mar. biol. Lab.* 14: 161-170.

CHENG, L., and LEWIN, R. A., 1967. — Goose barnacles (Cirripedia: Thoracica) on flotsam beached at La Jolla, California. *Fishery Bull. Fish. Wild. Serv. U.S.* 74: 212-217.

CRISP, D. J. 1967. — Chemoreception in cirripedes. *Biol. Bull. mar. biol. Lab. Woods Hole* 133: 128-140.

——, and SOUTHWARD, A. J., 1961. — Different types of cirral activity of barnacles. *Phil. Trans. R. Soc.* B243: 271-308.

DARWIN, C., 1851. — *A monograph on the subclass Cirripedia. The Lepadidae or pedunculate cirripedes.* London: Ray Society.

EVANS, F., 1958. — Growth and maturity of the barnacles *Lepas hilli* and *Lepas anatifera. Nature* 182: 1245-1246.

FOSTER, B. A., 1978. — The marine fauna of New Zealand: barnacles (Cirripedia Thoracica). *N.Z. Oceanogr. Inst. Memoir* 69: 1-60.

GRUVEL, A., 1893. — Contribution à l'étude des Cirrhipèdes. *Arch. Zool. exp. gén.* 1: 401-610.

HORN, M. H., TEAL, J. M., and BACKUS, R. H., 1970. — Petrol lumps on the surface of the sea. *Science* 168: 245-246.

HOWARD, G. K., and SCOTT, H. C., 1959. — Predacious feeding in two common gooseneck barnacles. *Science* 129: 717-718.

JONES, E. C., 1968. — *Lepas anserifera* Linné (Cirripedia Lepadomorpha) feeding on fish and *Physalia*. *Crustaceana* 14: 312-313.

LANG, W. H., 1979. — Larval development of shallow water barnacles of the Carolinas (Cirripedia:Thoracica) with keys to naupliar stages. *N.O.A.A. Tech. Rpt. N.M.F.S. Circular 421. U.S. Dept. Commerce,* pp. 1-39.

LOCKWOOD, A. P. M., 1968. — *Aspects of the Physiology of Crustacea.* Edinburgh: Oliver and Boyd.

NEWMAN W. A., 1972. — Lepadids from the Caroline Islands (Cirripedia Thoracica). *Crustaceana* 22: 31-38.

NILSSON-CANTELL, C. A., 1921. — Cirripeden Studien. Zur Kenntnis der Biologie, Anatomie und Systematik dieser Gruppe. *Zool. Bidrag, Uppsala* 7: 75-395.

PATEL, B., 1959. — The influence of temperature on the reproduction and moulting of *Lepas anatifera* L. under laboratory conditions. *J. mar. biol. Ass. U.K.* 38: 589-597.

PETRICONI, V., 1969. — Vergleichend anatomische Untersuchungen an Rankenfussern. I. Die mundwerkzuege von *Lepas anatifera* (L). *Zool. Jb. Anat. Ont.* 86: 67-83.

SKERMAN, T. M., 1958. — Rates of growth in two species of *Lepas* (Cirripedia). *N.Z. Jl. Sci.* 1: 402-411.

SOUTHWARD A. J., 1957. — On the behaviour of barnacles. III. Further observations on the influence of temperature and age on cirral activity. *J. mar. biol. Ass. U.K.* 36: 323-334.

STUBBINGS, H. G., 1963. — Cirripedia of the tropical South Atlantic coast of Africa. *Res. Sci. Exped. oceanogr. Belg. Eaux Cot. Afr. Atlant. Sud.* 3(10): 1-39.

——, 1975. — *Balanus balanoides.* L.M.B.C. Memoir No. 37. Liverpool: University Press.

UTINOMI, H. 1968. — Pelagic, shelf and shallow water Cirripedia from the Indo-West Pacific. *Vidensk, Meddr. dansk. naturh. Foren.* 131: 161-186.

ZULLO, V. A., 1963. — A preliminary report on systematics and distribution of barnacles (Cirripedia) of the Cape Cod region. *Publ. Mar. Biol. Lab. Woods Hole.* 33pp.